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AMITOSIS IN THE EGG FOLLICLE CELLS OF THE CRICKET.[1]

EDWIN G. CONKLIN.

THAT type of nuclear division known as amitosis or direct division which was once supposed to be universal is now known to occur so exceptionally that all teachers of cytology will welcome, I think, the announcement of its existence in great beauty and profusion in a common animal of wide distribution. It is this consideration which leads me to publish the observations here recorded which were first made more than six years ago.

It has been long known that one of the most favorable objects for the study of amitosis is to be found in the egg follicle cells of certain insects (*cf.* Carnoy '85, Korschelt '86, Preusse '95); in most if not all of these cases, however, it occurs only occasionally and must be searched for among many cells which do not show it. However in the case of the common crickets, *Gryllus pennsylvanicus*, *abbreviatus* and *domesticus*, every follicle cell in the enlarged portion of the ovarial tubes shows some stage or other in the process of direct nuclear division, and these cells are so easily prepared and they show every step of the division with such diagrammatic clearness that they cannot fail to become favorite objects for class demonstration.

A few words as to the structure of the ovarial tubes of the cricket and as to the best methods of preparing them for the demonstration of amitosis may not be out of place. If a mature female cricket, which can readily be distinguished from the male by the presence of the long median ovipositor, be torn in two it will be seen that a large part of the abdomen is occupied by the ovarial tubes which are arranged in two masses, one on either side of the body; these tubes are attached behind to the right and left oviducts and in front, by long slender filaments to the walls of the dorsal vessel. In fixing these masses of egg tubes it is advisable to tease them apart, otherwise the fixing fluids may not penetrate to the interior of the masses or the tubes may be difficult to isolate afterwards. Almost any modern fixing fluid will give good results, though I have had most success with picro-acetic (Boveri), picro-sulphuric (Kleinenberg) and Zenker's fluid. After hardening in alcohol the ovarial tubes may be stained from five to ten minutes in picro-hæmatoxylin[1] and then mounted entire; such tubes show beautifully not only the follicle cells in various stages of division but also the egg cells in different stages of growth. However, for the accurate study of the amitosis it is necessary to remove portions of the follicle by means of needles; this can readily be done after the tubes have been stained and dehydrated and while they are in the clearing fluid. These pieces of the follicle can then be mounted in balsam and, if desirable, can be studied under an immersion lens, though the nuclei are so large that all the details of the division can be made out with a magnification of from 125 to 300 diameters. It is advisable to double stain those tubes from which the epithelium is to be stripped, in picro-hæmatoxylin followed by a weak solution of eosin, or with acid fuchsin and methyl green (Auerbach's formula) in order to bring out the sharp contrast between the chromatin and the nucleoli.

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[1] From the Zoölogical Laboratory of the University of Pennsylvania.

Each ovarial tube of the cricket consists of a number of sections, all of which except the first contain ova in various stages of growth. These sections are, Fig. 1, (*1*) the terminal filament, a thread of considerable length but of small diameter which serves to attach the tube to the walls of the dorsal vessel; (*2*) an enlarged section, the terminal chamber, which contains ovogonia and young ovocytes which are not arranged in a linear series; (*3*) a varying number of small ovocytes or eggs which are arranged in linear series but are not completely separated from one another by constrictions of the tube; (*4*) a section in which the egg cells are separated by deep constrictions, the epithelial cells growing all the way through the tube and thus form-

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[1]	
Delafield's hæmatoxylin	10 cc.
Distilled water	40 cc.
Kleinenberg's picro-sulphuric (stronger) . .	10 drops.

ing partitions between the eggs; in this section all the eggs are of approximately the same diameter, but the lower ones are much longer than the upper ones; (5) a section consisting of two or three eggs, each succeeding one being about four times the volume of the preceding and all being enormously larger than any of the ova in the other sections of the tube. Finally each of these tubes is attached to one of the two oviducts, through which the ripe ova escape.

In all sections of the tube the egg cells are covered by epithelial cells; in the second and third sections these cells are relatively large and their nuclei are far apart; in the fourth section they are small and the nuclei are closely crowded together, at the same time many of the nuclei come to lie beneath the surface layer and some of them seem to be completely isolated in the yolk, to the formation of which they probably contribute. In the second, third and fourth sections of the tube the cells increase rapidly by division, the nuclei always dividing by mitosis; in these sections I have never seen a case of amitosis. The ovarial tube is not as the name might lead one to believe a tube composed of follicle cells through which the ova

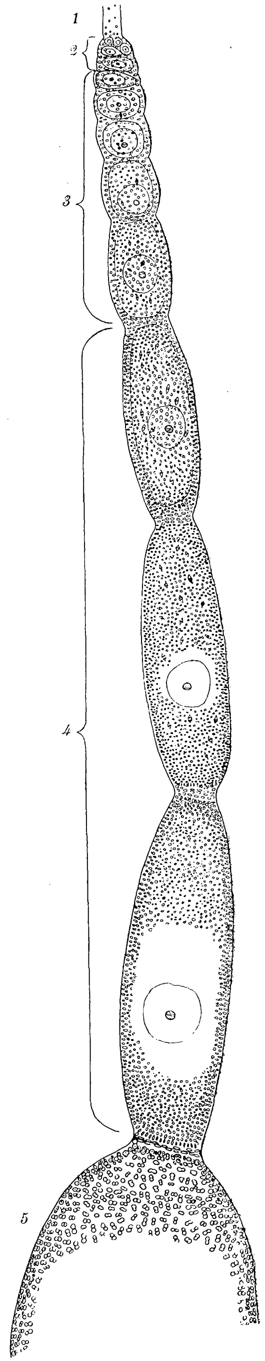


FIG. 1.—Ovarial tube of cricket; *1*, terminal filament; *2*, ovarial chamber; *3*, section in which individual eggs are not separated by follicle cells; *4*, section in which eggs are completely separated by the ingrowth of follicle cells; *5*, last section of tube containing two or three large ova; in this section all nuclei of follicle cells are in process of amitotic division. × 62.

descend from one section to another; on the other hand in all the sections below the ovarial chamber each ovum is permanently surrounded by its own follicle cells which descend with the ovum and increase in number with its growth in size. The extent to which these follicle cells multiply can be estimated by comparing their number in the fourth section with that in the second, which would indicate that the increase cannot be less than a hundred fold. In the fifth section mitosis rarely if ever occurs, but here all the nuclei are found to be in some stage of amitosis. In spite of the fact that all of the follicle cells of this section are found in process of division the increase in the number of the cells and nuclei in the successive segments of this section is not great, not nearly as great as in the preceding sections. Coincidently with the great growth of the egg cells in this section the follicle cells and their nuclei grow rapidly in size though they do not increase rapidly in number; this would indicate that the process of amitosis is here a very slow one, which may, perhaps, account for the fact that it is to be seen in all the nuclei.

Figures 2 and 3 represent portions of the follicle from the region of the ovarial chamber and just below it; both show characteristic mitoses but no evidence of amitosis in any of the cells.

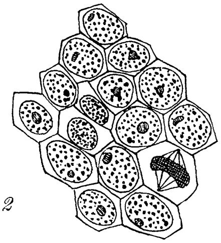


FIG. 2.—Fragment of epithelium from the ovarial chamber (section 2) showing mitosis. × 900.

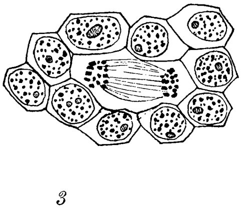


FIG. 3.—Fragment of epithelium from section 3 of the egg tube, showing mitosis. × 900.

Figures 4–8 however taken from the greatly enlarged portion (fifth section) of the tube show every nucleus in process of amitotic division. In this division, as is shown in all the figures named but particularly well in Fig. 5, the nucleolus first elongates and then becomes constricted in the middle. The elongation and constriction of the entire nucleus follows after that of the nucleolus. After the nucleolus has completely divided into two the nucleus also divides, but although two separate daughter nuclei are frequently found in these follicle cells I have never seen any indication of a division of the cell body. After the first amitotic division of the nucleus the nucleolus in many cases elongates again and divides in an axis at right angles to that of its preceding division so that two nucleoli are present in each of the daughter nuclei, Fig. 5. The daughter nuclei may also become elongated and even constricted in the middle, but I have never seen them completely divided into four nuclei within the single cell. This division of the nucleolus and nucleus is almost always an equal one and it usually occurs in a plane parallel with the surface of the epithelium.

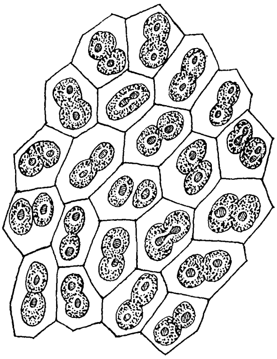


Fig. 4.—Fragment of follicular epithelium from the first egg in the fifth section of the egg tube. × 333.

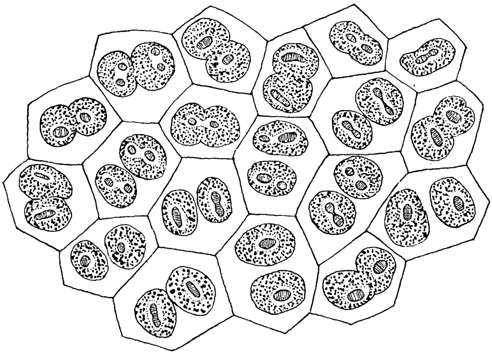


Fig. 5.—Follicular epithelium from the second egg in the fifth section of the egg tube. × 333.

It is interesting to note that this case of amitosis almost exactly corresponds to the type described by Remak in '55. He maintained that "cell division proceeds from the centre toward the periphery. It begins with the division of the nucleolus, is continued by simple constriction and division of the nucleus and is completed by division of the cell body and membrane" (Wilson, :00, p. 63). For a score of years after Remak's work this was supposed to be the prevalent if not universal type of cell division. Then it gradually came to be recognized that karyokinesis or mitosis was the usual form of nuclear division and that amitosis was comparatively rare, in fact its very existence was called in question. In particular the type of Remak which begins with the division of the nucleolus was found to be most unusual, being as Wilson says (:00, p. 115) "one of the rarest forms of cell division (!)." Such preliminary divisions of the nucleolus have been described by Carnoy ('85) in the egg follicle cells of the mole-cricket, Gryllotalpa, and also in Lithobius and in Geotrupes, by Wheeler ('89) in the follicle cells of Blatta, by Hoyer ('90) in the intestinal cells of the nematode, Rhabdonema, by Korschelt ('95) in the intestine of the annelid,

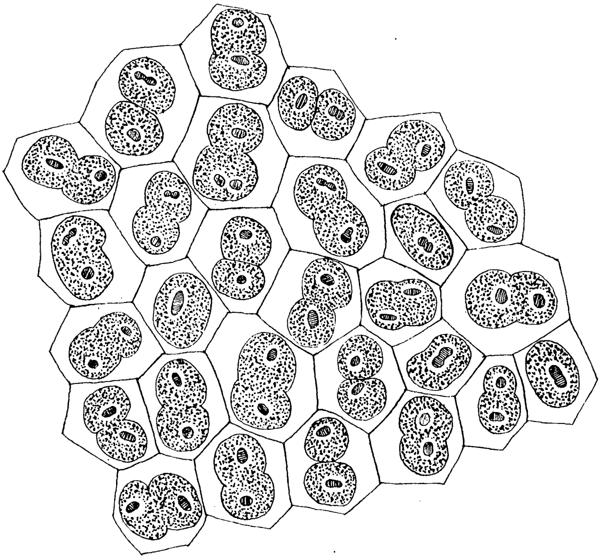
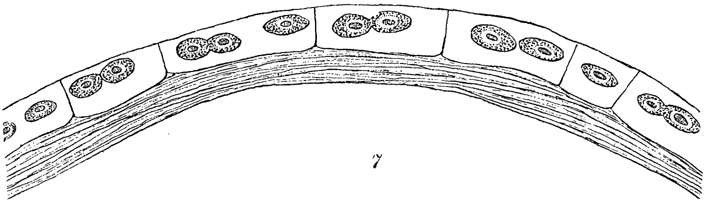


FIG. 6.—Follicular epithelium from the third and largest egg in the fifth section of the egg tube. × 333.

Orphryotrocha, by de Bruyne ('97) in the follicle cells of several insects and by Montgomery ('98) in the peritoneal cells of Polydora. In none of these cases however is it found so abundantly and so plainly as in the follicle cells of the cricket. I have examined the follicle cells of a number of insects and am surprised to find how infrequent amitosis is in most of them. In the mole cricket, as in all the species of true crickets which I have examined it occurs in great profusion, but in the case of the former the division of the nucleus is brought about by a deep constriction on one side only of the nucleus. In the grasshopper the nuclei are spherical and not bilobed and rarely show any indication of amitosis and the same is true of several other insects which I have examined.

In most cases of amitosis the nucleolus does not divide and a regular division of the nucleolus into two equal parts, preceding an equal division of the nucleus such as is found in the cricket is an occurrence of such rarity as to render it unusually interesting. Another peculiar feature of these divisions is that the nucleolus is always surrounded by a clear faintly-staining area free from chromatin. This area is probably not the result of shrinkage since it is found after all of the best methods of fixation which show no traces of shrinkage in other parts. This clear zone around the nucleolus elongates with the elongation



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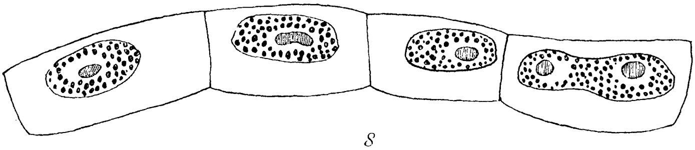

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FIG. 7.—Section through the follicular epithelium and underlying chorion of the smallest egg in the fifth section of the egg tube. × 333.

FIG. 8.— Section through the follicular epithelium of the largest egg in the ovarium tube. × 333.

of the nucleolus and after the division of the latter it also divides (Fig. 5). In the elongation, constriction and division of the nucleolus into equal parts and in the presence of this clear peripheral layer which also elongates and divides, the nucleolus in the follicle cells of the cricket is very unlike ordinary nucleoli, while in both of these respects it resembles an intranuclear centrosome or "centro-nucleolus." Whether this resemblance is merely a superficial one without significance (analogy) or a fundamental likeness (homology) cannot be affirmed without a more extensive study of the structures in question, particularly of the fate of the centrosomes which are found in the mitotic divisions in the upper portions of the tube. If it should turn out that these nucleoli are really comparable to centrosomes their peculiar structure and form of division would find a ready explanation.

The biological significance of amitosis in this case cannot be a matter of much doubt. These amitotic divisions are found only in the terminal segments of the ovarial tubes at which time the follicle cells are actively secreting the chorion (Fig. 7). After the formation of the chorion and before the egg is laid these cells completely degenerate and disappear. A follicle cell which has once divided by amitosis never again divides mitotically; in fact no mitoses are ever found in this terminal section of the tube. These facts all indicate that the amitotic division is, in this case, one of the last functions of these cells and that it is therefore an accompaniment of cellular senescence and decay.

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